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THE LEIOCEPHALUS (LACERTILIA, IGUANIDAE) MUS. COMP. ZOOL.

OF THE SOUTHERN BAHAMA ISLANDS

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HARVARD UNIVERSITY

The southern Bahama Islands are inhabited by two allopatric species of the West Indian lizard genus Leiocephalus: L. inaguae Cochran on Great Inagua Island, and L. arenarius Barbour (psammodromus auct., see p. 159) on various islands on the Turks and Caicos banks. These two species are both characterized by possession of a distinct lateral longitudinal fold between the fore- and hindlimbs, a feature which they share with L. melanochlorus Cope and L. schreibersi Gravenhorst from Hispaniola, L. macropus Cope and L. raviceps Cope from Cuba, and L. loxogrammus Cope from the Bahamian islands of Rum Cay and San Salvador. Since I (Schwartz, 1966 and MS) recently reviewed the status of the two Hispaniolan species with lateral folds, and since at the same time (MS) I compared L. schreibersi with both L. inaguae and L. arenarius, it is now appropriate to present the data gathered from this adjunct study as a unit dealing exclusively with the two southern Bahamian forms.

I visited Great Inagua Island and the Turks and Caicos banks islands in the company of David C. Leber. Material we collected is in the Albert Schwartz Field Series (ASFS). In addition to these specimens, I have had access to material in the American Museum of Natural History (AMNH); Museum of Comparative Zoology (MCZ); Museum of Zoology, University of Michigan (UMMZ); and United States National Museum (USNM). For the loan of these specimens I wish to thank the respective curators and their assistants—Charles M. Bogert and George W. Foley, Ernest E. Williams, Charles F. Walker, and Doris M. Cochran and James A. Peters. Paratypes of new forms have been placed in these collections and in the University of Illinois Museum of Natural History (UIMNH). Holotypes of three new forms have been deposited in the Carnegie Museum (CM). The illustrations are the work of Mr. Leber, and I want to thank him for their execution.

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GEOGRAPHY

The three areas occupied by *Leiocephalus* in the southern Bahamas are Great Inagua, the Caicos Islands, and the Turks Islands. Great Inagua lies on its own bank and is some 80 miles north of the north-western portion of Hispaniola and some 50 miles northeast of the extreme eastern extremity of Cuba. Little Inagua Island lies five miles northeast of Great Inagua, and is separated from it by a deep channel.

The Caicos Islands, along with the Turks Islands, were formerly dependencies of Jamaica but are now politically (as well as geographically and faunistically) associated with the Bahama Islands. The Caicos group is a series of islands of various sizes on a single bank, oriented in an arc bowed to the north, the greatest diameter of which (between West Caicos and Seal Cays) is about 60 miles. The major islands on the Caicos Bank, from west to east are: West Caicos, Providenciales, North Caicos, Grand Caicos, East Caicos, South Caicos, and the Amber-

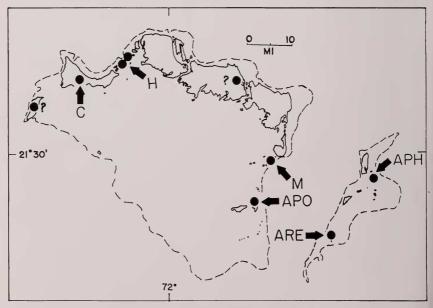


Fig. 1. Map of the Caicos (left) and Turks (right) bank islands. The limits of the banks are shown by a dashed line. The subspecies of *Leiocephalus arenarius* are indicated as follows: ARE, *arenarius*; APH, *aphretor*; APO, *apocrinus*; M, *mounax*; H, *hyphantus*; C, *cacodoxus*. Questioned localities indicate the occurrence of the species (subspecies indeterminate) on West and Grand Caicos. Stubb Cay, Ft. George Cay, and Sugar Loaf Island are not mapped. See text for comments.

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Leiocephalus of the Southern Bahama Islands

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gris Cays. Grand Caicos is the largest of these. The Caicos Rank is separated to the northwest from Mayaguana Island by the Caicos Passage, and lies about 70 miles north of west-central Hispaniola.

Separated from the Caicos Bank by the deep Turks Island Passage is the Turks Bank, on which lie the Turks Islands. These islands are oriented in the northeast-southwest direction, and the bank has a maximum length of about 40 miles. There are only three major Turks Islands (Grand Turk, Salt Cay, and Sand Cay), but there are innumerable smaller islets and rocks studded on the bank, especially between Grand Turk and Salt Cay. To the east the Turks Bank is separated from the Mouchoir Bank (which presently has no extensive exposed land) by the Mouchoir Passage. To the south lies Hispaniola, about 85 miles away. Despite the deep channels between Inagua and the Caicos and Turks banks, the 1000-fathom line unites them into a single land mass.

Aside from the presence of Leiocephalus on these three islands and island groups, their herpetofauna has some similarities (as well as some striking differences). None has any amphibians. Great Inagua has Aristelliger barbouri Noble and Klingel, and another species of Aristelliger (as vet unnamed; Hecht, 1951:24) occurs on one islet on the Caicos Bank. Great Inagua has an endemic species of Sphaerodactylus (with Hispaniolan affinities), whereas Grand Turk has two species (one with Bahamian, the other with Hispaniolan, affinities), and the Caicos Bank has one sphaerodactyl. Anolis scriptus Cope occurs in all three areas, and additionally on Mayaguana to the north. Cyclura occurs on both the Turks and Caicos banks, but is absent from Great Inagua. Great and Little Inagua have an endemic Ameiva with distant Hispaniolan affinities. Mabuya occurs on the Caicos and Turks banks, but is absent from Inagua. A Tropodophis with Bahamian affinities occurs on Great Inagua, and the distinct species T. greenwayi Barbour and Shreve occurs on the Caicos Bank although absent from the Turks Bank. Epicrates (with Cuban and/or Hispaniolan affinities) is presumed to have occurred on Great Inagua (the genus is known today on Sheep Cay off Great Inagua), has not been reported from the Caicos Bank islands, but is represented by a distinct form (Epicrates chrysogaster) on some of the Turks Islands (Ambergris Cays; ?Grand Turk). Great Inagua has an endemic subspecies of the Bahamian Alsophis vudii, but the genus is absent from the Turks and Caicos banks. Finally, Great Inagua has the endemic Chrysemys malonei. In general, the herpetofauna is an extremely depauperate Hispaniolan one, with some strikingly distinct endemic species. At least Aristelliger, Mabuya, Epicrates, and

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Chrysemys have been or are at present associated nomenclatorially with relatives to the south on Cuba and/or Hispaniola, whereas only the Great Inagua *Tropidophis canus* Cope and *Alsophis vudii* Cope have their most immediate relatives in the Bahama Islands.

Systematic Review

Leiocephalus inaguae Cochran, 1931

Leiocephalus inaguae Cochran, 1931, Jour. Washington Acad. Sci., 21: 39 (type locality—Man of War Bay, Great Inagua Island, Bahama Islands; holotype—USNM 81277).

DEFINITION: A species of *Leiocephalus* characterized by a combination of: (1) moderate size (males to 90 mm., females to 74 mm. snout-vent length); (2) presence of distinct sexual dichromatism; males can be distinguished from females by the presence of a pair of enlarged postanal scales; (3) a distinct lateral fold between the fore- and hindlimbs, with much smaller scales in the fold; (4) dorsal scales keeled and imbricate, ventral scales imbricate, smooth, and weakly cuspidate, with from two to four cusps which are often limited to the more central portion of the free margin of each scale; (5) median dorsal crest scales enlarged, strongly overlapping, and slightly lower than median dorsal caudal scales, 65 to 77 in occiput-vent distance; (6) one-half midbody scales 27 to 35; (7) supraoculars usually 7/7; (8) loreals 3 to 8; (9) temporals 10 to 14; (10) supraorbital semicircles usually complete; (11) parietals usually in contact; (12) median posterior azygous scale between second pair of median head scales absent; (13) modally 4 median head scales and 3 prefrontal scales. Hemipenis unknown.

VARIATION AND DISCUSSION: L. inaguae shows the following measurements and scale counts: dorsal crest scales between occiput and vent, 65-77 (mean 70.0), dorsal crest scales between occiput and axilla, 19-30 (mean 24.8), dorsal crest scales on trunk, 40-53 (mean 45.3), onehalf midbody scales, 27-35 (mean 30.5), subdigital fourth toe tricarinate scales 23-29 (mean 25.1), loreals 3-8 (mean 4.7), temporals 10-14 (mean 12.7), supraoculars 7/7 (11 specimens), 6/6 (5), 6/7 (4), 7/8 (8), 8/8 (2), 8/9 (2), 9/9 (1), 8/6 (1), semicircles usually complete (61.6 per cent), and parietals usually in contact (77.8 per cent). The prefrontal row consists of 3 or 4 scales (mode 3), the median head scales vary between 4 and 9 (mode 4), and the frontoparietal row has from 3 to 5 scales (mode 4). Both prefrontal and frontoparietal rows are most often complete, with only one lizard of 38 having the prefrontal row incomplete and six of 37 lizards with the frontoparietal row incomplete. The largest male has a snout-vent length of 90 mm., the largest female 74 mm.

L. inaguae is strongly sexually dichromatic. In males, the dorsum is tan with a series of about ten darker, brownish transverse rectangles or dumbbells between the nape and the sacrum. The lateral ends of these dumbbells abut against vague and yellowish dorsolateral stripes. Along the sides are a series of brownish squares, corresponding precisely to the dorsal dumbbells, each lateral square sending a brown bar onto the creamy abdomen. These ventrolateral brownish bars have brick-red and silver scales admixed. Anteriorly, the lateral squares, rather than being brown, are solid and velvety black. As many as the first five anterior lateral squares are so colored, but the largest male examined has only two black lateral blotches, and a slightly smaller male has only one (above the axilla). It is apparent that the number of black lateral squares or blotches is not correlated with size. Possibly it is correlated with geography, but the material at hand is too scanty and from too few localities to demonstrate it. The dorsal dumbbells may continue onto the base of the tail, gradually giving way to a series of brown caudal chevrons (with their apices pointed posteriorly) and finally to mere brown tail bands which are incomplete ventrally. The color of the head is uniform with that of the back and lacks any darker spotting. The limbs are tan to brownish, the forelimbs regularly paler than the hindlimbs, and both fore- and hindlimbs are heavily dotted or flecked with cream. There is some reddish pigment in the groin. The lateral fold has a series of creamy ovals along its length between the limbs in smaller males, but these disappear with increase in size. The smallest male having the lateral black squares anteriorly has a snout-vent length of 71 mm. Smaller males (snout-vent length from 41 mm. to 56 mm.) lack the lateral black markings. The throat pattern consists of a pair of dark brown diagonal lines which do not join on the gular midline, followed by about four longitudinal dark brown lines. This entire pattern is rather obscured because the gular ground color is also dark brown. In addition, the inter-line spaces are much flecked and dotted with cream scales. In the largest male, the throat pattern has practically disappeared, and the entire throat is a medium brown without prominent dark markings. In young males the throat pattern is somewhat more diagrammatic than in adult males, but even in the smaller specimens, the throat pattern is not bold since the lines are a dull drab brownish, rather than dark brown, and the throat ground color is dull grayish.

Females are like males dorsally, with a series of darker brown dumbbells or rectangles between yellowish dorsolateral stripes. The sides have a series of brown squares matching the position of the dorsal dumbbells, but none is black as in males. The lateral folds are marked with a series of cream ovals for their entire lengths, and in contrast to males, these ovals persist even into the largest females. The ventrolateral bars extending onto the abdomen are tan to gray, and more or less of the same color as the dorsum. The female throat pattern is like that of males in a general fashion, but is much more indistinct. All lines tend to be very fragmented, and in some females all that remains is a paramedian pair of longitudinal brownish lines, the rest of the throat being covered with irregular brownish and paler mottling and stippling. The throat ground color is tannish to dark gray or brownish, and is additionally irregularly striate with creamy to whitish streaks, so that the entire throat pattern is very obscure.

As I have previously pointed out (Schwartz, MS), L. inaguae females resemble female L. schreibersi in most details except for the throat pattern in inaguae (schreibersi lacks a throat pattern in either sex). Male inaguae, however, differ rather strikingly from schreibersi, the two most conspicuous features being the heavily patterned throat and the black anterolateral blotches in inaguae. Although I consider L. inaguae a L. schreibersi derivative (see Schwartz, MS, and below in the present paper), the former is so distinctive in these features of coloration and pattern that it merits specific ranking.

Noble and Klingel (1932:19-21) gave a rather detailed account of Klingel's observations on L. inaguae made during the three months that he was forced to remain on the island. My own observations more or less confirm those of Klingel. The species is not especially abundant on Inagua, although smaller individuals were observed in almost all exposed (in contrast to wooded) situations. At the lighthouse at Southwest Point L. inaguae was especially common, and large males (which were rarely encountered elsewhere) were seen and collected there readilv. About the lighthouse there were abundant abandoned building materials and large rocks, which the lizards frequented. Specimens were secured on the north coast (Union Creek), south coast (Conch Shell Point), and along the western shore of the island, and occasional smaller individuals were encountered near the salt pans which make up a large portion of the center of Great Inagua. In summary, my impression is that the lizards, although not completely shunning the non-coastal regions, were more abundant close to the shoreline, possibly because there they find more rocks, driftwood, and other suitable cover for both diurnal and nocturnal retreats.

SPECIMENS EXAMINED: Bahama Islands, Great Inagua, 13 mi. N. E. Conch Shell Point, 1 (ASFS 10402); 2 mi. W. Conch Shell Point, 13 (ASFS 10353-10365); Conch Shell Point, 2 (ASFS 10369-10370); lighthouse, Southwest Point, 10 (ASFS 10337-10346); 0.5 mi. S. Matthewtown, 7 (ASFS 10330-10336); 12 mi. N. E. Matthewtown, 1 (ASFS 10401); mouth of Union Creek, 5 (ASFS 10391-10395).

Leiocephalus arenarius Barbour, 1916

Leiocephalus arenarius Barbour, 1916 (nec Steironotus arenarius Tschudi, 1845), Proc. Biol. Soc. Washington, 29: 217 (type locality—Bastion Cay, Turks Islands; holotype—MCZ 11948).

Leiocephalus psammodromus Barbour, 1920 (substitute name for L. arenarius Barbour, 1916), Copeia, no. 85: 73.

DEFINITION: A species of Leiocephalus characterized by a combination of: (1) moderate size (males to 105 mm., females to 83 mm. snout-vent length); (2) strong sexual dichromatism; males can be distinguished from females by the presence of a pair of enlarged postanal scales; (3) a distinct fold between the fore- and hindlimbs, with much smaller scales in the fold; (4) dorsal scales imbricate and keeled, ventral scales imbricate, smooth and weakly denticulate; (5) median dorsal crest scales enlarged, not strongly overlapping, lower than median dorsal caudal scales, 56 to 81 in occiput-vent distance; (6) one-half midbody scales 28 to 56; (7) supraoculars usually 6/6; (8) loreals 4 to 14; (9) temporals 10 to 18; (10) supraorbital semicircles more often complete than not; (11) parietals more often not in contact; (12) median azygous scale between posterior pair of median head scales absent; and (13) median head scales 3 to 12, mode variable by populations. The hemipenis of L. arenarius is rather small, extending the length of about seven subcaudal scales. The sulcus is deep and prominent, and is formed laterally by an extensive longitudinal membranous flap from the base of the organ to near its tip. The non-sulcate surface has a series of about five flounces which extend around the organ to near the sulcus and which gradually merge into a series of about seven or eight rows of calyces. The tip of the hemipenis is smooth, rather deeply bifurcate, and much crenulated. The sulcus extends into a cordate terminal area. A raised calyculate area extends down the non-sulcate surface, and ends at the level of the flounces on the non-sulcate surface.

Etheridge (1966) has demonstrated that the nominal genus Leiocephalus Gray, 1827, is composed of two distinct genera, of which one (Leiocephalus) is exclusively Antillean and the other (Ophryoessoides Duméril, 1851) is continental. By this action, arenarius Tschudi, 1845, is placed in the genus Ophryoessoides (see Etheridge, 1966: 88) and arenarius Barbour, 1916, once more becomes available for the Leiocephalus of the southern Bahama Islands. L. psammodromus Barbour, 1920, was proposed by Barbour as a substitute name for these lizards, with the same holotype and type locality as L. arenarius Barbour.

Leiocephalus arenarius arenarius Barbour, 1916

TYPE LOCALITY: Bastion Cay, Turks Islands (see discussion below).

DIAGNOSIS: A subspecies of *L. arenarius* characterized by a combination of pale dorsal coloration, with three lateral nuchal brown blotches reduced and discrete, the three most anterior (two nuchal, one axillary) dorsal transverse bars prominent, throat pattern much fragmented and indistinct, and supraorbital semicircles usually complete.

DISTRIBUTION: Bastion Cay and Sand Cay, Turks Islands (fig. 1).

variation and discussion: The type locality of *L. arenarius* is presently unlocatable. Bastion Cay is not shown on any modern charts of the Turks Islands, and questioning natives there while I visited the islands yielded negative results. It is apparent that this name has fallen into disuse since the earlier years of this century. Dr. Williams at the Museum of Comparative Zoology likewise has had no success in checking the old records and Barbour's correspondence concerning the type series. Consequently, it is perfectly possible that I associate the specimens from Sand Cay incorrectly with the material from Bastion Cay. In any event, the two lots are much alike in coloration and pattern; they do differ from one another in several modal scale characters as shown below, the most striking being the reversal of semicircle completeness. However, in such instances, it must be remembered that there are only seven specimens from Bastion Cay, whereas there are 17 from Sand Cay. Additional material might well eradicate these modal differences.

L. a. arenarius is the palest of the subspecies. I have not seen the nominate form in life, so that my remarks on coloration are based exclusively on preserved specimens.

Males are pale yellowish-tan dorsally, with usually only two nuchal and one axillary dark brown transverse bars prominent against the pale ground color. At times the following two (postaxillary) dorsal bars are also rather prominent, but only rarely so bold as the three anterior bars. The interspaces between the bars, as well as the balance of the dorsum, are covered by very fine brown speckling and stippling, and the trunk shows hardly any indication of the transverse bars which occur in some of the other subspecies. Each anterior dark dorsal bar has a concomitant lateral dark blotch or spot, so that there is a series of three dark spots on the neck and above the axilla. These blotches are not confluent, and are separated by the folds of skin which lie between them. In one specimen (USNM 81338) the lateral spots are asymmetrical. At times, the interspaces between the anterior bars are so heavily stippled that the bars are made out only with difficulty. In males from Sand Cay

the limbs are stippled with dark brown, whereas the two males from Bastion Cay do not show this character, the limbs being more or less dark grayish-brown with paler spotting. The upper surface of the head is yellowish-tan with much paler and darker marbling, most prominent on the temples. The throat pattern is composed of the isolated fragments of two pairs of brown diagonal lines (fig. 2). One male (USNM 81339) has the lines more complete than the other males, but they are still not bold and dark. Behind the diagonal lines and extending onto the chest are a few brownish dots or flecks, always well separated from one another. The belly is immaculate pale, and the under side of the limbs is vaguely flecked with a few scattered brownish markings. The tail is unicolor yellowish-tan above, and without chevrons.

Females are somewhat darker than males, and have a series of about 10 to 12 brownish transverse bars—often constricted medially to form dumbbells—which are outlined with pale flecks. In general, the head is not marbled with pale, but there are some brownish markings on the supraocular scales. The sides have a series of brownish squares which correspond to the dorsal transverse bars, but none of these lateral squares is dark brown or black and thus not strongly contrasting with the lateral ground color. The limbs are tan, flecked with paler tone. The lateral fold is not marked by a series of ovals between the limbs, and the upper side of the tail is chevronate (basally) to banded with darker brown to the tip. The lower sides are variously marbled, stippled, or flecked, and about six or seven short ventrolateral bars, extending toward the ventral midline, are barely indicated; these bars do not approach the ventral midline and are restricted to the extreme lateral limits of the venter. The throat pattern of females consists of two pairs of gray and complete diagonal lines. Behind the lines is an area of logitudinal dashes which in turn gives way to dense gray spotting on the chest. Some females show this pattern to a less intense degree, and one (USNM 81330) has the diagonal lines joined to one another by longitudinal lines, thereby giving a reticular effect. The female throat pattern is more complete than the fragmented pattern of the throats of males.

The series from Bastion Cay consists of two males and five females, of which two are very tiny (snout-vent lengths 34 mm.). The scale counts for this series are: dorsal crest scales between occiput and vent, 65-72 (mean 68.6), dorsal crest scales between occiput and axilla, 25-29 (mean 27.4), dorsal crest scales on trunk, 37-45 (mean 41.2), one-half midbody scales, 39-44 (mean 40.4), subdigital fourth toe tricarinate scales 23-27 (mean 25.7), loreals 7-10 (mean 8.0), temporals 14-16

(mean 15.2), supraoculars 6/6 in all specimens, semicircles more often incomplete (57.2 per cent), and parietals usually (85.7 per cent) not in contact. The prefrontal row consists of 3 to 5 scales (mode 4), the median head scales vary between 3 and 6 (mode 6), and the frontoparietal row has 4 or 5 scales (mode 5). The prefrontal row most often is complete (one of seven lizards has the row incomplete), whereas the frontoparietal row more often is incomplete (three of five lizards). The largest male (the holotype) has a snout-vent length of 105 mm. (the largest representative of *L. arenarius* I have examined), and the largest female has a snout-vent length of 77 mm.

The series from Sand Cay consists of six males and 11 females. The largest male has a snout-vent length of 85 mm., the largest female 71 mm. The Sand Cay specimens are considerably smaller than those from Bastion Cay. Their scale counts are: dorsal crest scales between occiput and vent, 56-76 (mean 66.5), dorsal crest scales between occiput and axilla, 18-37 (mean 27.1), dorsal crest scales on trunk, 36-48 (mean 40.3), one half midbody scales, 38-53 (mean 43.1), subdigital fourth toe tricarinate scales 23-29 (mean 26.4), loreals 6-10 (mean 8.4), temporals 13-17 (mean 14.8), supraoculars 6/6 (14 specimens), 5/6 (2), semicircles more often complete (87.5 per cent), and parietals usually (92.9 per cent) not in contact. The prefrontal row consists of 4 to 6 scales (mode 5), the median head scales vary between 5 and 7 (mode 5), and the frontoparietal row has from 3 to 6 scales (mode 5); all specimens have the prefrontal row complete, whereas four of 11 lizards have the frontoparietal row incomplete.

The major scale difference between the Bastion Cay and Sand Cay samples include the higher percentage of complete semicircles in the Sand Cay sample (87.5 per cent vs. 43.8 per cent), and the different modalities of the head scales (4 prefrontals-6 medians-5 frontoparietals = 4-6-5, vs. 5 prefrontals-5 median-5 frontoparietals=5-5-5). In having more lizards with incomplete rather than complete frontoparietal rows, the Bastion Cay sample differs not only from the Sand Cay sample, but also from all other samples of *L. arenarius*. It is difficult to assess the significance of the differences between the Bastion and Sand cays populations on the basis of such limited material from the type locality. They are at least very alike in pattern and coloration, and the scale differences may merely be sample artifacts. In addition, the precise locality of Bastion Cay renders the identity of the Bastion Cay and Sand Cay material problematical.

SPECIMENS EXAMINED: Turks Islands, Bastion Cay, 7 (MCZ 11948—holotype; MCZ 11949-11952 + one untagged specimen—paratypes; USNM 81987—paratype); Sand Cay, 17 (MCZ 54194-54195, USNM 81329-81343).

Leiocephalus arenarius aphretor, new subspecies

HOLOTYPE: CM 40602, an adult male, from Long Cay, southeast of Grand Turk Island, Turks Islands, one of a series collected by David C. Leber on January 29, 1961. Original number 10908.

PARATYPES: ASFS 10909-10912, ASFS 10915-10918, UIMNH 61668-61671, USNM 157907-157910, same data as holotype; MCZ 54191-54193, same locality as holotype, G. Underwood, July 9, 1955; USNM 81303-81328, same locality as

holotype, P. Bartsch, August 1, 1930.

DIAGNOSIS: A subspecies of *L. arenarius* characterized by a combination of yellow dorsum with five lateral nuchal, axillary, and postaxillary black blotches extensive but discrete, five (two nuchal, one axillary, two postaxillary) dorsal transverse bars prominent, throat pattern fragmented but black rather than brown and more complete than that of *L. a. arenarius* and supraorbital semicircles more often incomplete.

DISTRIBUTION: Known only from Long Cay, Turks Islands (fig. 1).

DESCRIPTION OF HOLOTYPE: An adult male with the following measurements and counts: snout-vent length 95 mm., tail ca. 140 mm., complete; dorsal crest scales between occiput and vent 61, dorsal crest scales between occiput and axilla 24, trunk dorsal crest scales 37, one-half midbody scales 42, fourth toe scales 23/26, loreals 7, temporals 17, supraoculars 7/6; prefrontal row complete, 5 scales; 5 median head scales; frontoparietal row incomplete, 5 scales; semicir-

cles complete; parietals not in contact.

Coloration of holotype: Dorsum yellow with a series of five velvety black transverse bars, two on the neck, one across the supra-axillary region, and two postaxillary, each connected laterally to a large, more-or-less circular black blotch on each side; remainder of dorsum with vague indications of about five more transverse bars posteriorly to the sacrum, but none black or bold, and merely indicated by rather dull brownish areas, heavily marbled with black which also extends onto the sides. Upper surface of head brown, very heavily flecked with yellow, and very dark brown on the temples and neck anterior to the first nuchal transverse black bar, and supraoculars suffused with darker brown. Forelimbs not paler than hindlimbs, both medium brownish, forelimbs heavily dotted with black, hindlimbs dotted with black and yellow, although black dots much less conspicuous on hindlimbs. Tail with two dumbbell-shaped brown areas basally, but remainder of tail brown and without pattern except for about five distal brownish chevrons. Throat ground-color yellow, and much clouded with grayish purple, with black fragments of the two diagonal lines very disjunct and incomplete, followed by widely scattered dark brown flecks onto the chest (fig.3). Venter pale yellow, with about four very short ventrolateral rows of pearly yellow scales extending from the lower sides toward the ventral midline. Under side of limbs yellowish with scattered brownish and pearly yellowish scales.

VARIATION: The series of 38 *L. a. aphretor* shows the following counts:

dorsal crest scales between occiput and vent, 61-81 (mean 69.3), dorsal crest scales between occiput and axilla, 16-31 (mean 25.0), dorsal scales on trunk, 37-51 (mean 44.4), one-half midbody scales, 38-56 (mean 44.8), subdigital fourth toe tricarinate scales 22-28 (mean 25.7), loreals 6-9 (mean 7.6), temporals 12-18 (mean 15.3), supraoculars 6/6 (33 specimens), 5/6 (1), 6/7 (8), 7/7 (1), 7/5 (1), semicircles more often incomplete (68.2 per cent), and parietals usually not in contact (95.3 per cent). The prefrontal row consists of 3 to 5 scales (mode 4), the median head scales vary between 4 and 9 (mode 5), and the frontoparietal row has from 3 to 6 scales (mode 4). One of 46 specimens has the prefrontal row incomplete, and ten of 43 specimens have the frontoparietal row incomplete.

The holotype is representative of the males. The five black transverse bars, joined narrowly to the five lateral black blotches, are a constant feature. The throat ground color is yellow, but the yellow pigment is restricted to yellow blotches due to the random occurrence of grayish purple pigment on the throat. The throat pattern, although somewhat variable in extent and at times somewhat more complete than that described for the holotype, is always irregularly fragmented, lacks the complete configuration of the two diagonal lines, and may even be very obscure. The posterior throat and chest are speckled with brownish dots. The fore-and hindlimbs are always the same in color, and the hindlimbs are dotted and flecked with black and yellow.

Females have the dorsal ground color yellowish tan to dull tan. There is a series of about ten transverse blackish to gravish brown bars between the occiput and the sacrum. In other specimens, some additional bars are crowded between the primary bars, resulting in a total as high as 15 (ASFS 10915). The bars are outlined by tan edges or tan-to-cream flecks, and the axillary bar is often somewhat more bold and black than all other dorsal bars. There are no black lateral blotches, the sides being tannish to brown with only very vague indications of brownish lateral squares. The pale ovals along the lateral fold are inconspicuous. The tail is chevronate proximally or banded distally, and may have additional cream flecking on its upper surface (USNM 157908). The throat pattern is dull gray and is quite variable. Basically the two diagonal pairs of lines are present, but may be incomplete and/or grossly fragmented or joined intra se by short branches to give a gular reticulum. In some females the throat pattern is very obscure and barely demonstrated. Behind the diagonal lines there is an area of short longitudinal gray dashes which in turn yields to heavy gray dotting extending onto the

chest. The venter is grayish, and there are about four ventrolateral lines with dull pearly white scales extending from the lower sides toward the midventral line. The forelimbs are pale above with brown (rather than black) flecking and marbling, and the hindlimbs are brown above with some diffuse dark brown and cream marbling.

comparisons: Male L. a. aphretor differ from the nominate subspecies in dorsal color and pattern, since the latter has only three anterior transverse bars and three discrete lateral blotches, and the former has five in each case. In both subspecies the lateral blotches remain discrete and are not fused with one another. L. a. arenarius is a much paler lizard dorsally than aphretor, and the dorsal stippling and markings posterior to the last transverse bar in arenarius are much more conspicuous than those in aphretor. The male throat patterns of the two races are similar, but the pattern of aphretor is much darker and bolder thant that of arenarius (despite the grayish purple suffusion on the throat ground color in aphretor) and in general is more complete. Females of the two races are similar, but the tendency toward reticulation of the throat pattern in aphretor occurs only rarely in arenarius. Females of the latter race also generally have the throat pattern more completely expressed.

The only major difference in scales between these two subspecies is the modal condition in *aphretor* of having the semicircles incomplete. In *arenarius* the semicircles are usually complete (assuming that the Sand Cay and Bastion Cay samples represent the same subspecies). The modal head scale condition of 4-5-4 in *aphretor* differs from 4-6-5 and 5-5-5 in the two *arenarius* samples.

REMARKS: L. arenarius is known only from three islands on the Turks Bank—Bastion Cay, Sand Cay, and Long Cay. It is absent from Grand Turk (where Leber and I spent one week without seeing the species) and apparently absent from Salt Cay. The lizards may well occur on other lesser Turks Islands, but as presently known, they occupy two islands which are removed some 17 miles from one another. The isolation of the Long Cay population is referred to in the name aphretor, from the Greek for "without social ties."

Leiocephalus arenarius apocrinus, new subspecies

HOLOTYPE: CM 40601, an adult male, from Big Ambergris Cay, northwest side, Caicos Islands, one of a series collected by David C. Leber and Albert Schwartz on January 13, 1961. Original number 10616.

PARATYPES: ASFS 10613-10615, ASFS 10617, ASFS 10620-10623, UIMNH

61672-61674, USNM 157911-157913, same data as holotype; MCZ 42053-42060, "Ambergris Cay," March 1936, J. C. Greenway.

DIAGNOSIS: A subspecies of *L. arenarius* characterized by a combination of yellow dorsum usually with four lateral nuchal and axillary black blotches which are somewhat confluent, especially anteriorly, four or five (three nuchal, one axillary, and at times one postaxillary) prominent dorsal transverse bars, throat pattern dark gray to blackish, relatively more complete but still somewhat irregular and fragmented and with an additional transverse bar on the first and second sublabial scales, and supraorbital semicircles most often complete.

DISTRIBUTION: Known definitely only from Big Ambergris Cay, on the Caicos Bank, but probably occurring as well on adjacent Little Ambergris Cay to the west (fig. 1).

DESCRIPTION OF HOLOTYPE: An adult male with the following measurements and counts: snout-vent length 99 mm., tail 80 mm., tip regenerated; dorsal crest scales between occiput and vent 68, dorsal crest scales between occiput and axilla 23, trunk dorsal crest scales 45, one-half midbody scales 46, fourth toe scales 27/28, loreals 11, temporals 14, supraoculars 7/7; prefrontal row complete, 4 scales; 6 median head scales; frontoparietal row incomplete, 4 scales; semicircles complete; parietals not in contact.

Coloration of holotype: Dorsum yellow with a series of four velvety black transverse bars, three on the neck, one across the supra-axillary region, each connected laterally to a large, more-or-less circular black blotch on each side, the two anteriormost blotches on the neck rather broadly fused with one another, the more posterior two less broadly so; remainder of dorsum with two much less clearly defined and much broken postaxillary bars and the vaguest remnants of five other bars, increasingly less clear, before the sacrum; dorsum behind axillary transverse bar much overlaid with irregular black scrawls and marbling; interspaces between anterior four bars also heavily marbled with black. Upper surface of head brownish, with much black and yellow dotting and marbling on the temples continuous with anteriormost lateral nuchal blotch, and supraoculars suffused with darker brown. Lower sides brown, heavily stippled and marbled with darker brown to black. Forelimbs pale tan, heavily flecked with black; hindlimbs distinctly darker, mottled with yellowish gray and black, the black much less conspicuous than on the forelimbs, and almost forming a reticulum. Tail with two very obscure darker dumbbells basally, otherwise patternless brownish on unregenerated portion. Throat ground color mottled gray and yellow, with the more anterior pair of brownish diagonal lines almost complete, but second pair represented by a series of dashes basically arranged in a diagonal pattern; a brownish transverse bar across the chin at the level of the first and second sublabials; scattered but regular brownish spotting onto the chest and underside of the forelimbs posterior to second pair of diagonal line remnants (fig. 4). Venter gravish vellow with four dull ventrolateral bars extending toward the midventral line from the lower sides and lacking any pearly or iridescent scales. Underside of hindlimbs yellowish with scattered brownish and pearly yellow scales.

VARIATION: The series of 22 *L. a. apocrinus* shows the following counts: dorsal crest scales between occiput and vent, 63-78 (mean 70.0), dorsal crest scales between occiput and axilla, 21-29 (mean 24.5), dorsal scales

on trunk, 39-52 (mean 45.7), one-half midbody scales, 35-47 (mean 42.2), subdigital fourth toe tricarinate scales 25-29 (mean 27.2), loreals 6-12 (mean 8.3), temporals 12-16 (mean 14), supraoculars 6/6 (15 specimens), 6/7 (4), 7/7 (3), 7/8 (1), semicircles more often complete (60.9 per cent), and parietals equally in contact or not. The prefrontal row consists of 3 to 6 scales (mode 4), the median head scales vary between 4 and 10 (mode 6), and the frontoparietal row has from 4 to 7 scales (mode 5). Four of 22 specimens have the prefrontal row incomplete, and one of 20 specimens has the frontoparietal row incomplete. The largest male has a snout-vent length of 101 mm., the largest female 83 mm.

The paratypic males are as described for the holotype. The dorsal ground color is yellow, and there are regularly three nuchal transverse black bars indicated. Most often the bars are complete. Occasional specimens have a fifth (postaxillary) transverse bar, but this is exceptional. The lateral black blotches are large and more or less discrete. If joined to one another, the juncture is effected by narrow bands of black pigment which cross the folds of skin on the neck. The dorsum posterior to the dark anterior nuchal bands is variously mottled and stippled with black or brown, and any posterior transverse bars are much obscured or completely obliterated by the added dark dorsal pigmentation. Anteriorly, the interband spaces are heavily stippled with black and brown. On the neck anterior to the nuchal bands this stippling, along with added yellow dotting, covers the upper temporals and parietals. The lower temporals are very dark brown to black. This irregular temporal dark blotch is often confluent with the most anterior nuchal blotch. The lower sides are brown, heavily dotted and marbled with black. Although the holotype lacks prominent ventrolateral bars extending onto the venter, other males show these bars prominently, as well as pearly yellow scales. The throat ground color is cream to faintly yellow, and much suffused with gravish pigment. The throat pattern consists of the most anterior pair of diagonal lines as discrete units, followed by remnants (which may yield almost a complete unit) of the second pair of diagonal lines. There is always a transverse brown bar at the level of the first and second sublabials. Behind the diagonal lines lies an area of brown dotting which extends onto the chest. An occasional male has the more central dots aligned into a pair of paramedian dashed lines, but these are never clear or continuous.

Females are drab brownish, with a series of about 12 or 13 transverse brown dumbbells outlined with cream dots along both their anterior and posterior margins. There are often three transverse dark bars on the neck, although this is not a constant feature of females. The sides are brown, with a few cream scales admixed. The female throat pattern is more complete than that of the males. The two dark gray diagonal pairs of lines are complete on a grayish ground. The transverse chin bar is present but obscure. Posterior to the diagonal lines is an area of large, closely approximated dark gray spots, which extends onto the chest and the under side of the forearms. The lower sides and the underside of the hindlimbs are also heavily dotted with rather large and appressed dark gray dots. There is no indication of ventrolateral bars extending onto the abdomen. The limbs are brown, the anterior pair has some dark brown dotting, and the posterior pair has some grayish spotting and blackish marking.

comparisons: The presence of three nuchal bars and rare occurrence of any postaxillary bars on the dorsum distinguishes male *L. a. apocrinus* from both the nominate form and *aphretor*. Of the races thus far described, the throat pattern of *apocrinus* is the most complete and the least fragmented and obscure. The additional presence of the short transverse chin bar likewise distinguishes *apocrinus*. Females of the latter are much like female *aphretor* except that they lack ventrolateral lines extending onto the abdomen. The dorsal color of male *apocrinus* resembles that of *aphretor* but is darker than that of *arenarius*.

In having the semicircles more often in contact, *apocrinus* resembles *arenarius* and stands in contrast to *aphretor*. The head scale formula of 4-5-5 differs from that of the previously described races. Of all the populations of *L. arenarius*, only *apocrinus* has an even distribution of contact and non-contact of parietal scales. The nearest approach is the sample from Long Cay near South Caicos, but here, despite the approximately equal numbers in both categories, the modal condition is lack of parietal contact.

REMARKS: The Ambergris Cays are a pair of islets which lie to the southwest of South Caicos near the southeastern tip of the Caicos Bank. Big Ambergris Cay, the easternmost islet, is xeric in the extreme, and Turk's Cap cactus is common. Parts of the island are hilly, especially the western side, but there are also flat grassy patches in the interior. *Cyclura carinata* is abundant in these interior areas, and *L. a. apocrinus* was common along the rocky, and at times steep, coastline. Whether *L. a. apocrinus* occurs also on the closely adjacent Little Ambergris Cay remains unknown. The latter island actually is larger

than Big Ambergris Cay and is much flatter. The channel between the two islands is only three feet deep and less than two miles wide.

Big Ambergris Cay is separated from Sand Cay in the Turks group by about 19 miles of deep water, and is about 28 miles from Long Cay, southeast of Grand Turk. In features of pattern and coloration, however, apocrinus resembles aphretor on Long Cay rather than arenarius on Sand Cay. The name apocrinus is derived from the Greek for "separated."

Leiocephalus arenarius mounax, new subspecies

HOLOTYPE: CM 40603, an adult male, from Long Cay, off Cockburn Harbour, South Caicos, Caicos Islands, one of a series collected by David C. Leber on Jan-

uary 12, 1961. Original number 10581.

PARATYPES: ASFS 10582-10587, ASFS 10599-10602, MCZ 81122-81127, UIMNH 61675-61680, same data as holotype; MCZ 54169, 54171-54184 + 19 untagged specimens, Long Cay, Caicos Islands, about July, 1955, G. Underwood; USNM 81399-81409, Long Cay, Caicos Islands, July 29, 1930, P. Bartsch; AMNH 76056-76060 + 43 untagged specimens, Long Cay, Caicos Islands, February 8-9, 1953, natives for G. B. Rabb and L. Giovannoli.

DIAGNOSIS: A subspecies of *L. arenarius* characterized by a combination of pale-to-bright yellow dorsum with five lateral nuchal, axillary, and postaxillary black blotches, the first three of which are usually confluent, five (two nuchal, one axillary, two postaxillary) transverse bars prominent, throat pattern black and consisting of two pairs of practically complete diagonal lines preceded by a transverse black bar at the level of the first and second sublabial scales, and supraorbital semicircles usually in contact.

DISTRIBUTION: Known only from Long Cay off Cockburn Harbour on South

Caicos, Caicos Islands (fig. 1).

DESCRIPTION OF HOLOTYPE: An adult male with the following measurements and counts: snout-vent length 89 mm., tail ca. 160 mm.; dorsal crest scales between occiput and vent 64, dorsal crest scales between occiput and axilla 22, trunk dorsal crest scales 42, one-half midbody scales 42, fourth toe scales 27/27, loreals 8, temporals 14, supraoculars 6/7; prefrontal row complete, 5 scales; 7 median head scales; frontoparietal row incomplete, 5 scales; semicircles incomplete; parietals not in contact.

Coloration of holotype: Dorsum bright yellow with a series of five velvety black transverse bars, two on neck, one across supra-axillary region, two post-axillary, the anteriormost three bars connected to an extensive lateral black nuchal-axillary blotch which represents the fusion of the three smaller blotches usually found in this position. The two postaxillary bars are unconnected to their own concomitant black lateral blotches which are large and extensive, but more or less discrete. Remainder of dorsum with about six faint and obscured blackish transverse bars before sacrum, the entire posterior dorsum overlaid with a heavy black mottling and/or stippling; interspaces between axillary and nuchal bars with little black stippling. Upper surface of head brown, with some black marbling on

temples. A rather bold broad cream line along the lateral fold between the limbs. Sides brown, stippled with black, lower sides below lateral fold paler brownish. Forelimbs pale tan, heavily dotted with black; hindlimbs brown, obscurely dotted with pale gray and dark brown to black. Tail brownish, slightly mottled with darker proximally, and vaguely banded with brownish distally. Throat ground-color cream, with two pairs of diagonal black lines, both slightly incomplete apically; anterior pair of diagonal lines with extensive deposition of black pigment laterally and on sublabials; a blackish transverse bar across chin at level of first and second sublabials; area behind diagonal lines occupied by both a vague third pair of diagonals plus black dotting onto chest, and extending to, and becoming brown on, under side of forelimbs (fig. 5). Venter pale yellow, with four or five ventrolateral bars with pearly yellow scales extending toward ventral midline. Underside of hindlimbs yellowish with brown dots and pearly whitish to yellowish scales.

Variation: The series of 98 *L. a. mounax* shows the following counts: dorsal crest scales between occiput and vent, 60-77 (mean 66.4), dorsal crest scales between occiput and axilla, 17-30 (mean 24.4), dorsal scales on trunk, 36-50 (mean 42.1), one-half midbody scales, 34-47 (mean 40.5), subdigital fourth toe tricarinate scales 22-31 (mean 27.2), loreals 5-14 (mean 8.2), temporals 11-16 (mean 13.7), supraoculars 6/6 (57 specimens), 5/6 (10), 6/7 (23), 7/7 (14), 7/8 (1), 8/6 (1), 7/5 (2), 6/8 (1), semicircles more often complete (57.3 per cent), and parietals more often not in contact (57.9 per cent). The prefrontal row consists of 4 to 7 scales (mode 5), the median head scales vary between 3 and 12 (mode 6), and the frontoparietal row has from 4 to 7 scales (mode 5); 13 of 113 specimens have the prefrontal row incomplete, and six of 99 specimens have the frontoparietal row incomplete. The largest male has a snout-vent length of 96 mm., the largest female 75 mm.

The five transverse black bars, of which two are nuchal and two postaxillary, are a common feature of the paratypic males. Occasionally a third postaxillary bar has approximately equal intensity as the bars before it, thus giving six prominent anterior black bars. The lateral black blotches are large and the first three are usually rather extensively fused; this fusion may also incorporate the postaxillary blotches to some degree, but this is not the modal condition. The dorsal ground color varies from pale to bright yellow, and the balance of the dorsum posterior to the transverse blotches is heavily overlaid with black mottling and stippling. In general there is relatively little black mottling in the anterior interbar spaces, and the head also is relatively free from both dark and pale dotting except for the dark temporal regions. The bellies vary from pale yellow to gray with the pearly scales in the ventrolateral

bars either gray or yellow. The black throat pattern, which occurs in most adult males, consists of two pairs of almost or fully complete diagonal lines, followed by an area of black dotting which extends onto the chest, and preceded by a short transverse grayish to blackish bar. There may be an indication of reticulation along the anterolateral margin of the first diagonal lines, but this feature is variable. In general, the throat pattern is bold and fairly complete. The forelimbs are consistently paler (tan) than the hindlimbs (brown), and are dotted prominently with black. The hindlimbs are vaguely spotted or marbled with pale gray and dark brown to black.

Females are dull gray to dull tan above, and have about ten darker brown dumbbells between the neck and sacrum. At times these dorsal figures are fairly conspicuous, and in other lizards they are hardly distinguishable from the ground color. The sides are brownish, and the fold-following series of cream to tannish ovals is present but not especially prominent. The throat pattern is gray and resembles that of the males in that there are two pairs of complete or almost complete wide diagonal lines (of which the anterolateral ends of the first pair may be involved in an incipient reticulum) followed by an area of gray longitudinal dashes or dots which extend onto the chest and under side of the forelimbs. The belly is grayish, often rather heavily dotted with pale gray. The five or six ventrolateral bars are at best short and inconspicuous, and often are lacking entirely. There is rather striking variation in the intensity and development of the chest pattern in females; some individuals (ASFS 10602) have the area, normally covered with dashes and dots posterior to the diagonal lines, covered rather with a densely packed series of longitudinal gray lines. Other females (MCZ 54181) may even have indications of a transverse (rather than longitudinal) gray line on the chest.

comparisons: L. a. mounax differs from all previously described races in having a black and virtually complete throat pattern in males, two nuchal and two postaxillary dorsal bars, and rather extensive confluence between at least the first three (nuchal and axillary) lateral blotches. In dorsal coloration, mounax is much darker than arenarius, but about equal to aphretor and apocrinus. The blotched throat ground color of apocrinus in contrast to the cream-to-yellowish throat color of mounax is another distinctive feature. In having modally complete semicircles, mounax differs from aphretor, which has the semicircles modally incomplete. The presence of two nuchal bars in mounax serves

also to distinguish it from *apocrinus*, which has three nuchal bars. The head scale formula of 5-6-5 differs from that of all other described subspecies. This difference may be most significant when compared with the counts of head scales in those races which are also represented by relatively large series: *aphretor* (4-5-4) and *apocrinus* (4-5-5).

REMARKS: Although *L. a. mounax* (the name is derived from the Greek for "alone") is abundant on Long Cay, it is absent from the closely adjacent South Caicos Island. Long Cay is separated from South Caicos by a channel much less than a mile in width. Such a peculiarity of distribution is difficult to explain, and can hardly be attributed to the presence of a rather extensive settlement with its domestic animals on South Caicos, since the greater portion of the latter island is uninhabited and wild. There are no specimens of *L. arenarius* from East Caicos, the next (and much larger) island to the north, but East Caicos has seldom been visited by collectors and remains little known. The species has been reported from the next island in the arc, Grand Caicos, but the two specimens available from there (USNM 81410 and 81411, from Lorimer Creek, Grand Caicos) are both immature and cannot be allocated to subspecies. All that can be said is that *L. arenarius* occurs on Grand Caicos.

L. a. mounax is closest geographically to L. a. apocrinus on Big Ambergris Cay. The distance separating the two islands is about eight miles, and both are on or near the eastern edge of the Caicos Bank.

Leiocephalus arenarius hyphantus, new subspecies

HOLOTYPE: UMMZ 126624, an adult male, from Pine Cay, Caicos Islands, one of a series collected by George B. Rabb on February 28, 1953. Original number VV1723.

PARATYPES: UMMZ 114516 (16 specimens) same data as holotype; USNM 81397-81398, same locality as holotype, July 24, 1930, P. Bartsch.

ASSOCIATED SPECIMENS: Caicos Islands, Water Cay, 4 (USNM 81393-81396); Stubb Cay (not mapped), 5 (USNM 81388-81392).

DIAGNOSIS: A subspecies of *L. arenarius* characterized by a combination of pale dorsum with one (axillary) to three (usually one axillary, two nuchal) discrete lateral black blotches, three (two nuchal, one supra-axillary) black velvety transverse dorsal bars followed by about six to ten less prominent but still distinguishable dorsal black bars or pairs of spots to the sacrum, throat pattern consisting of a black reticulum, and supraorbital semicircles usually in contact.

DISTRIBUTION: Known from Pine Cay and its associated Water and Stubb cays (fig. 1); specimens presumably from Ft. George Cay are more like the following subspecies, despite the fact that Ft. George Cay apparently lies between Pine Cay and Stubb Cay; see remarks.

DESCRIPTION OF HOLOTYPE: An adult male with the following measurements and counts: snout-vent length 87 mm., tail 93 mm., distal two-thirds regenerated; dorsal crest scales between occiput and vent and on trunk indeterminate; dorsal crest scales between occiput and axilla 26, one-half midbody scales 37, fourth toe scales-/29, loreals 8, temporals 13, supraoculars 5/5; prefrontal row complete, 6 scales; 7 median head scales; frontoparietal row complete, 5 scales; semicircles complete, parietals in contact.

Coloration of holotype: Dorsum tan (as preserved), with a series of five transverse black bars, two on neck, one across supra-axillary region, two postaxillary, followed by seven more-or-less complete (although fading posteriorly) bars or bar remnants to the sacrum; two lateral black blotches, matching the supraaxillary and first postaxillary dorsal bars; entire dorsum overlaid with brownish to blackish marbling or stippling, but less extensively so than in most other subspecies, so that the series of postaxillary transverse dorsal dark bars is still visible; interspaces between anterior bars stippled with black and some pale, but bars retain their identity. Upper surface of head brown, with some black on the medial portions of supraoculars; temporal region darkened (but not extensively so) with brown rather than black. A fairly conspicuous cream line down the lateral fold. Sides above fold tan stippled with brownish, below fold paler and gradually grading into ventral color. Forelimbs tan above, heavily dotted with black; hindlimbs brownish above, with both pale and dark gray dotting and marbling. Tail unmarked tan above on unregenerated portion. Throat ground color deep gray, with two complete pairs of black diagonal lines and a black transverse chin bar at level of first and second sublabials, the second pair of diagonals joined to a conspicuous black reticulum which covers the posterior part of the throat and gives way to scattered brownish dotting on the chest; first pair of diagonals connected reticularly to black sublabial dark markings, so that the general impression of throat pattern is a complex reticulum, with the exception of the isolated transverse chin bar (fig. 6). Venter pale gray (as preserved), with scattered pearly scales not forming ventrolateral rows. Under side of hindlimbs gray with heavy scattering of pearly scales and very faint and widely scattered brownish dots.

variation: The series of 19 paratypic *L. a. hyphantus* shows the following counts: dorsal crest scales between occiput and vent, 66-76 (mean 71.7), dorsal crest scales between occiput and axilla, 21-31 (mean 25.9), dorsal scales on trunk, 41-52 (mean 44.6), one-half midbody scales, 33-42 (mean 37.7), subdigital fourth toe tricarinate scales 25-30 (mean 27.1), loreals 5-10 (mean 7.5), temporals 10-15 (mean 12.9), supraoculars 6/6 (9 specimens), 5/5 (1), 6/7 (7), 7/7 (1), 7/5 (1), semicircles usually complete (88.9 per cent), parietals usually not in contact (82.4 per cent). The prefrontal row consists of 3 to 6 scales (mode 4), the median head scales vary between 3 and 10 (mode 5), and the frontoparietal row has 2 to 5 scales (mode 5). One lizard of 19 has the prefrontal row incomplete, and four lizards of 19 have the fronto-

parietal row incomplete. The largest paratypic male has a snout-vent length of 98 mm., the largest female 78 mm.

The paratypic series of L. a. hyphantus from Pine Cay consists of nine males and nine females. The males agree with the description of the holotype in both dorsal and throat pattern. The largest male (UMMZ VV1708) has the throat heavily clouded with dark gray and also flecked with whitish (as preserved) scales, but the throat pattern is black and still prominent. There are additional lines joining the diagonals, so that a reticulum is visible. Several other males have the throat ground color very dark also, but never so much as to obscure the dark and definitive throat pattern. Many males (UMMZ VVI718, VV1722, for instance) show the complete dorsal pattern of transverse bars or bar remnants as does the holotype, but other males (UMMZ VV1713, VV1708, for example) have the posterior bars more reduced, although their less obvious aspect is due to their own reduction rather than to the deposition of obliterative black pigment. Even in the most extreme case, the full suite of dorsal bars is present. Because of the reduction of dorsal dark obliterative stippling and marbling, some male L. a. hyphantus resemble the nominate race far to the east. The anterior dorsal barring consists of three prominent bars—the two nuchal and the supra-axillary. The lateral blotches are much reduced in extent, and are variable in number, the dorsal nuchal bars seldom having any prominent concomitant lateral black blotch. The postaxillary bars may or may not have a vague associated lateral blotch. If only one blotch is present, it is the one corresponding to the supra-axillary bar. In most other features of pattern the paratypes resemble the holotype, the exception being the presence in some males of more definitive ventrolateral bars with pearly scales extending toward the ventral midline—a condition which is absent in the holotype.

The Pine Cay females are drab brown dorsally with about ten to 12 dorsal bars or dumbbells, not outlined prominently with paler edges. In contrast to the patternless tails of the males, the tails of females are vaguely banded with darker brown for their entire length. The female throat pattern is like that of the males—black and boldly reticulate on a dark gray ground. Some females (UMMZ VV1720) show the reticulation less clearly, but in other females the net-like pattern is prominent. The area behind the diagonal lines is more or less longitudinally striate with dark gray to black, and the chest and sides of the venter are heavily dotted and spotted with gray. Ventrolateral bars are poorly expressed, the inter-bar areas being much dotted with gray. The pale line along the

lateral fold is not prominent, but its ovals may be discerned in some females. The sides above the lateral fold are dark brown, and apparently patternless.

comparisons: Because of its reticulate throat pattern in both sexes and the virtually completely patterned dorsum in males, *L. a. hyphantus* is readily distinguishable from all previously named subspecies. As noted above, some male *hyphantus* resemble some *arenarius* in lack of dorsal black obliterative stippling and marbling. These peculiarly marked male *hyphantus* can be easily distinguished from *arenarius* by the reticulate throat pattern. The name *hyphantus* is derived from the Greek for "woven," an allusion to the net-like or reticulate throat pattern.

In scales, *hyphantus* differs from *aphretor* in having the semicircles modally complete. The head scale formula of 4-5-4 is the same as that of *aphretor*, but differs from the formulae of other subspecies.

REMARKS: I have associated with the topotypical material specimens from Water Cay and Stubb Cay, both of which are closely adjacent to Pine Cay. The specimens from these two cays resemble *hyphantus* closely in all details, except that modally they have five (rather than four) frontoparietals, and there is a strong tendency for males to resemble the dorsally less prominently marked males from Pine Cay. The throat patterns of the Water and Stubb Cay specimens are identical with those from Pine Cay.

The only problematical specimens are a series (USNM 81384-81387) from Ft. George Cay, and the problem may well be one of incorrect locality due to insufficiently accurate charting of this section of the Caicos Bank. There is no detailed United States Hydrographic Office chart of the Caicos Bank. H. O. chart 948 includes this region (along with Hispaniola and many of the southern Bahamas), but in poor detail. A second chart (in Kline, 1966:270) is much more detailed—so much so in fact that it is difficult to rationalize the two interpretations of the Caicos Bank in this particular region! Aside from Parrot Cay (which is not involved in the present study), neither chart shows the same set of names -i.e., the H. O. chart has Stubb Cay and Ft. George Cay, whereas the Kline chart has Water Cay and Pine Cay. There is such a complex of islets between the large Providenciales Island on the west and the large North Caicos Island on the east, and there is such a confusing network of channels between these islets, that it is impossible to be sure which chart is correct or precisely to which cays the H. O. chart names should be applied on the Kline chart. Consequently, I am only roughly certain

of the locations of Pine, Water, and Stubb cays, and not at all certain about the location of Ft. George Cay.

The Ft. George Cay lizards are much closer in characters to the subspecies of L. arenarius on Providenciales than they are to those on Pine Cay. There are four possibilities: (1) Ft. George Cay lies between Water Cay and the eastern end of Providenciales (there are several unnamed cays shown on the Kline chart in this region); (2) the lizards did not come from Ft. George Cay, but the locality was so designated for want of another (possibly more accurate) name; (3) Ft. George Cay, despite its separation from Providenciales by the Pine Cay-Water Cay pair, does indeed have the same subspecies of L. arenarius as does Providenciales because of some accident of colonization; or (4) by convergence of characters, the lizards of Ft. George Cay may fortuitously have diverged from their adjacent relatives on Pine and Stubb cays to come to resemble the lizards on Providenciales. I consider the last possibility the least likely, and imagine that the confusion is simply the result of inadequate mapping and charting of the region with subsequent incorrect locality designations. In such a group of islets, it is not impossible to mistake one cay for another, especially when some are unmapped and unnamed, or when too much reliance is placed on names supplied by a native guide.

Leiocephalus arenarius cacodoxus, new subspecies

HOLOTYPE: MCZ 54185, an adult male, from Providenciales Island, Caicos Islands, one of a series collected by L. Franklin on July 31, 1955.

PARATYPES: MCZ 54186-54190, same data as holotype.

ASSOCIATED SPECIMENS: ?Ft. George Cay, 4 (USNM 81384-81387); Sugar Loaf Island (not mapped), 1 (USNM 81412).

DIACNOSIS: A subspecies of *L. arenarius* characterized by a combination of moderately dark dorsum with four or five lateral black blotches fused into a single black lateral band, five (two nuchal, one supra-axillary, two postaxillary) dorsal black bars which do not connect laterally with the black lateral blotch, remainder of dorsum without prominent bars or bar remnants and moderately stippled with dark, throat pattern consisting of a complete set of gray diagonal lines, often with a third pair of diagonals on the posterior portion of the throat, semicircles usually not complete, and parietals modally in contact.

DISTRIBUTION: Known certainly only from Providenciales Island and Sugar Loaf Island, Caicos Islands (fig. 1); occurrence on "Ft. George Cay" problematical—see discussion above.

DESCRIPTION OF HOLOTYPE: An adult male with the following measurements and counts: snout-vent length 89 mm., tail 100 mm., all but the basal quarter regenerated; dorsal crest scales between occiput and vent 75, dorsal crest scales between occiput and axilla 23, dorsal scales on trunk 52, one-half midbody scales

41, fourth toe scales 27/27, loreals 5, temporals 13, supraoculars 6/7; prefrontal row complete, 3 scales; 4 median head scales; frontoparietal row complete, 4 scales; semicircles incomplete, parietals in contact.

Coloration of holotype: Dorsum tan (as preserved) with a series of five transverse velvety black bars (two nuchal, one supra-axillary, two postaxillary), followed by four very vague pairs of moderately dark blotches to sacrum, the latter blotches much obliterated by brown stippling; a single large black blotch from the neck to behind the axilla, virtually continuous but showing some constrictions to confirm its quinquepartite origin; interspaces between anterior bars practically without black pigment so that the bars are especially prominent. Head tan above, without dark markings; temples without black or dark brown pigment, but some whitish temporal blotching ventrally. Lateral fold with a vague pale line. Sides above fold brownish, without conspicuous black stippling; lower sides brownish with only vague indications of ventrolateral pearly scales extending toward ventral midline. Forelimbs pale above, with brown dotting; hindlimbs darker above and with dark brown dotting fairly well defined. Tail unpatterned but with a few scattered light scales on unregenerated portion. Throat ground color clear and unclouded pale with three dark gray and discrete pairs of diagonal lines, the most anterior pair joined by a series of short lines to gray pigment on the infra- and sublabials; an area of widely spaced grayish brown dots, behind the third pair of diagonal lines, extending onto chest and undersides of the forelimbs (fig. 7). Venter pale with scattered pearly scales not forming ventrolateral bars. Underside of hindlimbs dotted with pearly and pale brown scales.

Variation: The series of seven *L. a. cacodoxus* (Providenciales and Sugar Loaf Island) shows the following counts: dorsal crest scales between occiput and vent, 68-76 (mean 71.2), dorsal crest scales between occiput and axilla, 23-29 (mean 26.8), dorsal scales on trunk, 42-52 (mean 44.3), one-half midbody scales, 32-41 (mean 36.7), subdigital fourth toe tricarinate scales 26-28 (mean 27.1), loreals 5-8 (mean 6.1), temporals 10-13 (mean 11.9), supraoculars 6/6 (4 specimens), 5/6 (1), 6/7 (1), 7/8 (1), semicircles usually incomplete (85.7 per cent), parietals usually in contact (71.4 per cent). The prefrontal row consists of 3 or 4 scales (mode 3), the median head scales vary between 4 and 7 (mode 4 or 6), and the frontoparietal row has 4 or 5 scales (mode 5). One of seven lizards has the prefrontal row incomplete, and no lizard has the frontoparietal row complete. The largest topotypic male has a snout-vent length of 89 mm., the largest female 71 mm.

Of the two adult and one juvenile males, one adult (MCZ 54186) and the juvenile (USNM 81412 from Sugar Loaf Island) agree very well in throat pattern with the holotype, the juvenile having the third pair of diagonal lines at least indicated, and the adult having the three pairs of diagonals fully expressed. The adult has the lateral blotches somewhat more discrete than the holotype, but there is fusion between the two

nuchal and axillary blotches. The second adult (MCZ 54190) has the single large fused lateral blotch, but the throat pattern is extremely fragmented. The three pairs of diagonal lines are present, but all—especially the third or extra pair—are broken. In other dorsal features, the two adults resemble the holotype.

Females of *L. a. cacodoxus* likewise are a peculiar lot. Two have a throat pattern like that of the males, but differing in color: pale gray rather than dark gray or black. The third (MCZ 54189) has all diagonals much obscured through the formation of a reticulum. All females have the posterior throat and chest heavily marked with rather large gray spots. Dorsally the females are dull brown with about eight transverse bars or dumbbells, barely outlined with some pale markings or isolated pale scales. The sides are brown, and the lateral fold pale ovals are moderately obvious. There is barely an indication of the ventrolateral grayish bars extending onto the venter.

comparisons: By virtue of its throat pattern, L. a. cacodoxus is readily distinguishable from its closest neighbor, L. a. hyphantus. In males, the latter has a complex reticulate throat pattern on a dark ground, the former a clearly delineated gray pattern of diagonals on a clear pale ground. Doubtless in life there are pigmental differences in this region as well. The solid black anterolateral blotch in cacodoxus contrasts with the obsolescent blotches in hyphantus. Of the other subspecies, in throat pattern cacodoxus most closely resembles mounax, but the extra set of diagonals and the lateral solid blotch will differentiate the two with ease. These two subspecies occupy islands at almost the two extremes of the Caicos arc.

The Ft. George Cay series has been discussed above. The three males and one female have the throat patterns so clearly like the topotypes of *cacodoxus*, rather than the heavily patterned throats of *hyphantus*, that lizards on this basis are clearly referrable to the former subspecies. The lateral blotches are discrete and do not form a single blotch, and on this basis the lizards are closer to *hyphantus*. I assign them to *cacodoxus*, but possibly they might be better regarded as intergrades between these two races on the basis of combination of characters. In favor of this intergradient interpretation is the fact that the semicircles are modally complete whereas the parietals are modally not in contact—precisely the condition in *hyphantus* in contrast to that in *cacodoxus*.

As far as head scalation is concerned, only *cacodoxus* and *aphretor* have the semicircles usually incomplete, and only *cacodoxus* has the

parietals modally in contact. The modal head scale formula of *cacodoxus* (3-4 or 6-5) is confusing and doubtless due to the small series involved. Of interest is the fact that in having a modal condition of three prefrontals and parietal contact, *cacodoxus* (inhabiting islands near the extreme western end of the Caicos Bank) resembles *L. inaguae*. *L. a. cacodoxus* is the only subspecies of *L. arenarius* which has these two conditions modally.

REMARKS: The name *cacodoxus* is derived from the Greek for "without fame" or "unknown," an allusion to seldom-visited Providenciales Island.

SPECIMENS FROM WEST CAICOS

Aside from the two immature L. arenarius from Grand Caicos already mentioned, there is a fine series of 15 specimens (AMNH 76047-76055 + six untagged specimens) from West Caicos which must likewise remain unassigned subspecifically. The latter series consists of four immature males (snout-vent lengths from 39 to 55 mm.) and 11 females. Since immature males are patterned and colored more or less like adult females, there is nothing distinctive about them. Since females lack the very prominent features of adult males, it would be improvident to base a subspecific name on a sample composed primarily of females and young males. However, the following points are suggestive. The throat pattern of the West Caicos females is like that of L. a. cacodoxus from nearby Providenciales (the two islands are separated by a channel about four miles in width). The throats are distinctive, however, in being heavily and extensively patterned, especially posterior to the third pair of diagonals (which are usually present). Some females show also some reticulation between the first and second pair of diagonals. Although these West Caicos females might be assigned to cacodoxus, it seems preferable to await the collection of adult males on West Caicos before stating definitely that they belong to the Providenciales subspecies.

DISCUSSION

I have recently (Schwartz, MS) suggested that *L. inaguae* and *L. arenarius* are derivative forms from the Hispaniolan *L. schreibersi*. The latter species is fairly widespread on Hispaniola and occurs on Ile de la Tortue off the northwestern Haitian coast (where it has an endemic subspecies). Since female *schreibersi* and female *inaguae* have some characteristics in common, I had originally considered that *inaguae* might



Fig.2. Throat of $L.\ a.\ arenarius,\ MCZ\ 11948,\ holotype,\ from\ Bastion\ Cay,\ Turks\ Islands.$

Fig. 3. Throat of $L.\ a.\ aphretor,\ {\rm CM}\ 40602,\ {\rm holotype},\ {\rm from}\ {\rm Long}\ {\rm Cay},\ {\rm Turks}$ Islands.

Fig. 4. Throat of $L.\ a.\ apocrinus,$ CM 40601, holotype, from Big Ambergris Cay, Caicos Islands.

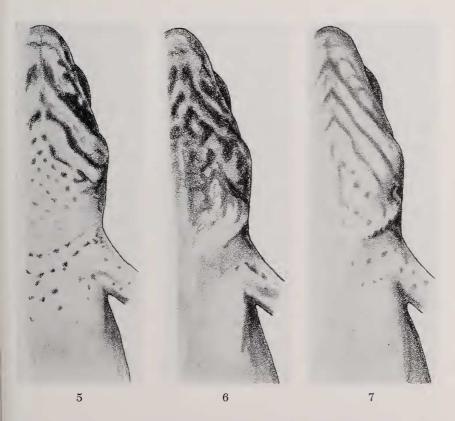


Fig. 5. Throat of $L.\ a.\ mounax$, CM 40603, holotype, from Long Cay, Caicos Islands.

Fig. 6. Throat of $L.\ a.\ hyphantus$, UMMZ 126624, holotype, from Pine Cay, Caicos Islands.

Fig. 7. Throat of *L. a. cacodoxus*, MCZ 54185, holotype, from Providenciales Island, Caicos Islands.

best be regarded as a subspecies of the Hispaniolan species. However, considering the radical pattern differences in the males of the two forms (and even though some of these pattern features in *inaguae* might be fairly readily derived from those of *schreibersi*), the degree of differentiation between *inaguae* and *schreibersi* seems to indicate a specific level of differentiation (when one views the genus as a whole) rather than a subspecific one.

This statement is even more true for *L. arenarius*. There are few resemblances between *arenarius* and *schreibersi*, other than the dorsal pattern in females and the presence of a lateral fold and its concomitant series of pale ovals. The latter feature occurs also in *L. melanochlorus* in southwestern Haiti and is a group feature for these four species (in contrast to the three other species with lateral folds—*macropus*, *raviceps*, and *loxogrammus*). The throat pattern of *arenarius*, despite its wide variation, never approaches the immaculate gray-to-purplish throat of *schreibersi* or the densely patterned throat of *inaguae*. In a general fashion, the *arenarius* throat pattern with its diagonal lines resembles that found in some subspecies of the Cuban *L. stictigaster* Schwartz (see Schwartz, 1964: 214, for illustrations), although this resemblance is surely fortuitous and should not suggest close relationships, since *stictigaster* lacks a lateral fold.

The two southern Bahamian species might be regarded as subspecifically related, although I feel that this is not the case. The modal occurrence in *L. a. cacodoxus* of some scale features which occur modally in *inaguae* as well, but not modally in other *arenarius* populations, might be interpreted as showing that *cacodoxus* is closest to the original prearenarius stock which arrived on the Caicos Bank from Great Inagua. But this flimsy evidence is unsupported by any other chromatic or pattern features in common, and is belied by the very striking differences in throat pattern between *inaguae* and *cacodoxus* (not to mention the balance of *L. arenarius* as well). It therefore seems inappropriate to combine *L. inaguae* with *L. arenarius*, or either species with *L. schreibersi*.

Derivation of both species from Hispaniola seems most plausible, but inaguae and arenarius must represent two old and independent invasions of the southern Bahamas and their banks. Intra-Bahamian derivation of one from the other is a possibility, but not a likely one. Since the two Hispaniolan and the two Bahamian species form an interrelated complex, this suggests that the place of origin of this group of lizards with lateral folds has been the north island of Hispaniola (see Williams,

1961, for usage), whence three distinctive species (melanochlorus, inaguae, arenarius) have been derived from a central one (schreibersi). Such a proposed history is even more plausible since melanochlorus occupies the south island of Hispaniola, inaguae Great Inagua, and arenarius the Caicos and Turks banks—all peripheral to the Hispaniolan north island.

The three other Leiocephalus with lateral folds—macropus and raviceps on Cuba, and loxogrammus on San Salvador and Rum Cay in the more northerly Bahamas—differ in several features from the Hispaniolan quartet. Indeed, despite the hiatus in their known ranges, raviceps and loxogrammus are extremely close to one another, and might best be regarded as only subspecifically related (I do not make this nomenclatorial change here, but merely suggest that it may be done in the future). Doubtless these three species represent a second center of evolution for Leiocephalus with lateral folds, of which one member has extended its range into the central Bahamas. The picture is slightly less diagrammatic in Cuba, since raviceps and macropus are sympatric in some areas, and at least macropus is island-wide in a broad sense. Both species show strikingly disjunct distributions on Cuba as well. A detailed discussion of these species and loxogrammus must await further study. It is sufficient at the moment to recognize that there are two basic groups of Leiocephalus with lateral folds, and that each group shows a reasonably cogent and compact distributional picture.

In my discussion of variation in *L. schreibersi* (MS), I point out that, although there were suggestions of subspecific differentiation in that species on the Hispaniolan mainland, no obvious patterns of variation can be ascertained. A new subspecies was described from Ile de la Tortue off the northwestern Haitian coast, but none was described from the Hispaniolan mainland. This stands in such striking contrast to the situation in *L. arenarius*, with at least six subspecies scattered over a much smaller and less physiographically diverse area, that some comment should be made, especially if *L. schreibersi* is considered the basic stock whence *L. arenarius* was derived.

I attribute the diversification of *L. arenarius*, in essence, to its habitation of the islands of two archipelagos. Populations are completely isolated from one another, and probably have been for some considerable length of time. This is especially true of the Caicos Bank populations in contrast to the Turks Bank populations, although there is no greater degree of differentiation between the lizards inhabiting these two major areas than between lizards from relatively nearby islands on the same

bank. On Hispaniola, L. schreibersi has rather rigid habitat requirements, and the species occurs more or less continuously where these habitat requirements are met. Thus, there is practical continuity between schreibersi populations of the south-central República Dominicana and those of the Presqu'île du Nord Ouest in extreme northwestern Haiti. The only exceptional situations are the isolated population in the Valle de Cibao in northwestern República Dominicana, and the four populations on the islands of the Siete Hermanos group in the same region. Continuity of habitat and range militate against subspecific differentiation. Presumably the Valle de Cibao and Siete Hermanos schreibersi have only recently been cut off from the remainder of the population (in the former case), or have recently invaded the offshore islands (in the latter instance), so that there has been insufficient time for constant variational patterns to have become established in these isolated populations. Since the Siete Hermanos populations have diverged to some extent intra se, these islet populations may have been separated longer from their Cibao relatives than the latter have been from their relatives to the west in Haiti. On the other hand, the extremes of pattern variation in L. arenarius indicate that this species has long been an inhabitant of the Turks and Caicos banks islands, and that various populations have been isolated from one another for sufficiently long periods to permit the formation and establishment of strikingly different subspecies.

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